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The diverse nature of island isolation and its effect on land bridge insular faunas

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Abstract

Aim: Isolation is a key factor in island biology. It is usually defined as the distance to the geographically nearest mainland, but many other definitions exist. We explored how testing different isolation indices affects the inference of impacts of isolation on faunal characteristics. We focused on land bridge islands and compared the relationships of many spatial and temporal (i.e., through time) isolation indices with community-, population- and individual-level characteristics (species richness, population density and body size, respectively).

Location: Aegean Sea islands, Greece.

Time period: Current.

Taxon: Many animal taxa.

Methods: We estimated 21 isolation indices for 205 islands and recorded species richness data for 15 taxa (invertebrates and vertebrates). We obtained body size data for seven lizard species and population density data for three. We explored how well indices predict each characteristic, in each taxon, by conducting a series of ordinary least squares regressions (controlling for island area when needed) and a meta-analysis.

Results: Isolation was significantly (and negatively) associated with species richness in 10 of 15 taxa. It was significantly (and positively) associated with body size in only one of seven species and was not associated with population density. The effect of isolation on species richness was much weaker than that of island area, regardless of the index tested. Spatial indices generally out-performed temporal indices, and indices directly related to the mainland out-performed those related mainly to neighbouring islands. No index was universally superior to others, including the distance to the geographically nearest mainland.

Main conclusions: The choice of index can alter our perception of the impacts of isolation on biological patterns. The nearly automatic, ubiquitous use of distance to the geographically nearest mainland misrepresents the complexity of the effects of isolation. We recommend the simultaneous testing of several indices that represent different aspects of isolation, in order to produce more constructive and thorough investigations and avoid imprecise inference.

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KEYWORDS

Aegean islands, body size, island area, island biogeography, population density, spatial isolation, species richness, temporal isolation

1 | INTRODUCTION

Isolation and area are the two main abiotic factors purported to affect insular evolutionary ecology and biogeography (Hamilton & Armstrong, 1965; Itescu, 2019; MacArthur & Wilson, 1967; Santos, Field, & Ricklefs, 2016; Whittaker & Fernández-Palacios, 2006). According to the dynamic equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967), island area and isolation determine species richness by affecting rates of extinction (mainly a function of area) and immigration (mainly a function of isolation). This theory predicts that species richness generally increases with island area and declines with isolation. The original dynamic equilibrium model (MacArthur & Wilson, 1963, 1967) regards area and isolation as equally important for determining species richness. Later studies suggested that diversification (i.e., cladogenesis) is another, in some cases the most, important factor determining species richness, especially in remote archipelagos, where colonization rates are low (Heaney, 2000; Rosindell & Phillimore, 2011; Whittaker, Triantis, & Ladle, 2008, cf. Ali & Meiri, 2019).

A large proportion of island biogeography studies focus on oceanic islands, although land bridge islands compose the vast majority of islands worldwide (Meiri, 2017). The dynamics of species assembly on land bridge islands are fundamentally different from those on oceanic islands because the former harbour life when they become isolated, whereas the latter start devoid of life (Itescu, 2019; Santos et al., 2016). According to the “general dynamic theory of island biogeography” (Whittaker et al., 2008), which deals principally with oceanic islands, geographical (i.e., spatial) isolation plays a key role in determining species richness on islands (Santos et al., 2016; Whittaker et al., 2008). Colonization is crucial on oceanic islands (Cabral, Whittaker, Wiegand, & Kreft, 2019), and poor dispersers are unlikely to reach very distant islands (Borges & Hortal, 2009). Subsequent modifications of the dynamic equilibrium theory of MacArthur and Wilson (1967) have also postulated a concomitant impact of isolation on extinction rates, which are reduced on near islands via meta-population “rescue” effects (Brown & Kodric-Brown, 1977). Consequently, on land bridge islands, which are often much closer to the source landmass, spatial isolation (i.e., the minimal geographical distance of a focal island from other landmasses) is expected by some to affect species richness only weakly (Case, 1975; Palmeirim, Vieira, & Peres, 2017). On such islands, richness has been shown to be determined mainly by community relaxation processes (i.e., species extinction driven by reduced carrying capacity of the landmass after its isolation; Case, 1975; Diamond, 1972; Foufopoulos & Ives, 1999; Foufopoulos, Kilpatrick, & Ives, 2011; Wilcox, 1978). Extinction (= “relaxation”) dynamics are time dependent (Brown, 1971; Whittaker, Fernández-Palacios, Matthews, Borregaard, & Triantis, 2017). Temporal isolation, the length of time

during which an insular biota has been shaped in isolation from other biotas, might therefore be more important than spatial isolation for land bridge islands. The longer an island has been isolated, the lower the richness will be, until an equilibrium is reached.

Island area is straightforward and relatively easy to estimate, but isolation is not. Indices of isolation that are based on the minimal distance of an island from another landmass or on the length of time for which it has been separated from other landmasses can be defined with respect to different landmasses. One can quantify isolation (either spatial or temporal) from the nearest mainland, the nearest mainland from which it acquired its fauna (see Materials and Methods), the nearest island, the nearest larger island, the landmass to which it was most recently connected, etc. (Figure 1). Other factors, such as surrounding landmass area, wind regimens, sea currents and habitat similarity between islands, may also contribute to the isolation of an island (Foufopoulos & Mayer, 2007; Weigelt & Kreft, 2013). In particular, the amount of surrounding land area was found to be very important for plant species richness (Diver, 2008; Weigelt & Kreft, 2013). This is another type of spatial isolation index; it indicates the amount of potential source area available within a defined radius around a focal island, while accounting for the shape of the focal island and the source landmasses. The larger the land area found within the radius, the less isolated an island is, and therefore the higher the species richness is expected to be (everything else being equal; Weigelt & Kreft, 2013). Although a multitude of potential isolation indices exists, studies that test and compare more than two indices (e.g., Itescu et al., 2018; Weigelt & Kreft, 2013) or examine composite isolation indices (e.g., Boyer & Jetz, 2010) are uncommon.

Despite the multifaceted nature of isolation, the distance to the geographically nearest mainland is by far the most frequently used index and is often the only one. This may be because the nearest mainland is usually assumed to be the richest gene pool and species source for a focal island (Weigelt & Kreft, 2013). This measure may also be popular because it is the easiest and most straightforward to calculate. But is it the most informative or powerful index? Diver (2008) and Weigelt and Kreft (2013) examined this for plant species richness, comparing a variety of spatial isolation indices, and found that it was not. Instead, other indices, such as the amount of surrounding land area and the distance from close larger islands, performed better. The response of species richness to environmental factors, however, often differs between animals and plants (Currie, 1991; Hawkins et al., 2003). The consistency of the effect of isolation on animal richness, or traits, was never explored thoroughly across different metrics. Millien-Parra and Jaeger (1999) showed that neighbouring islands were more important than the mainland as sources of mammal island colonizers. In other cases, none of the examined isolation indices, including the distance to the nearest mainland, was

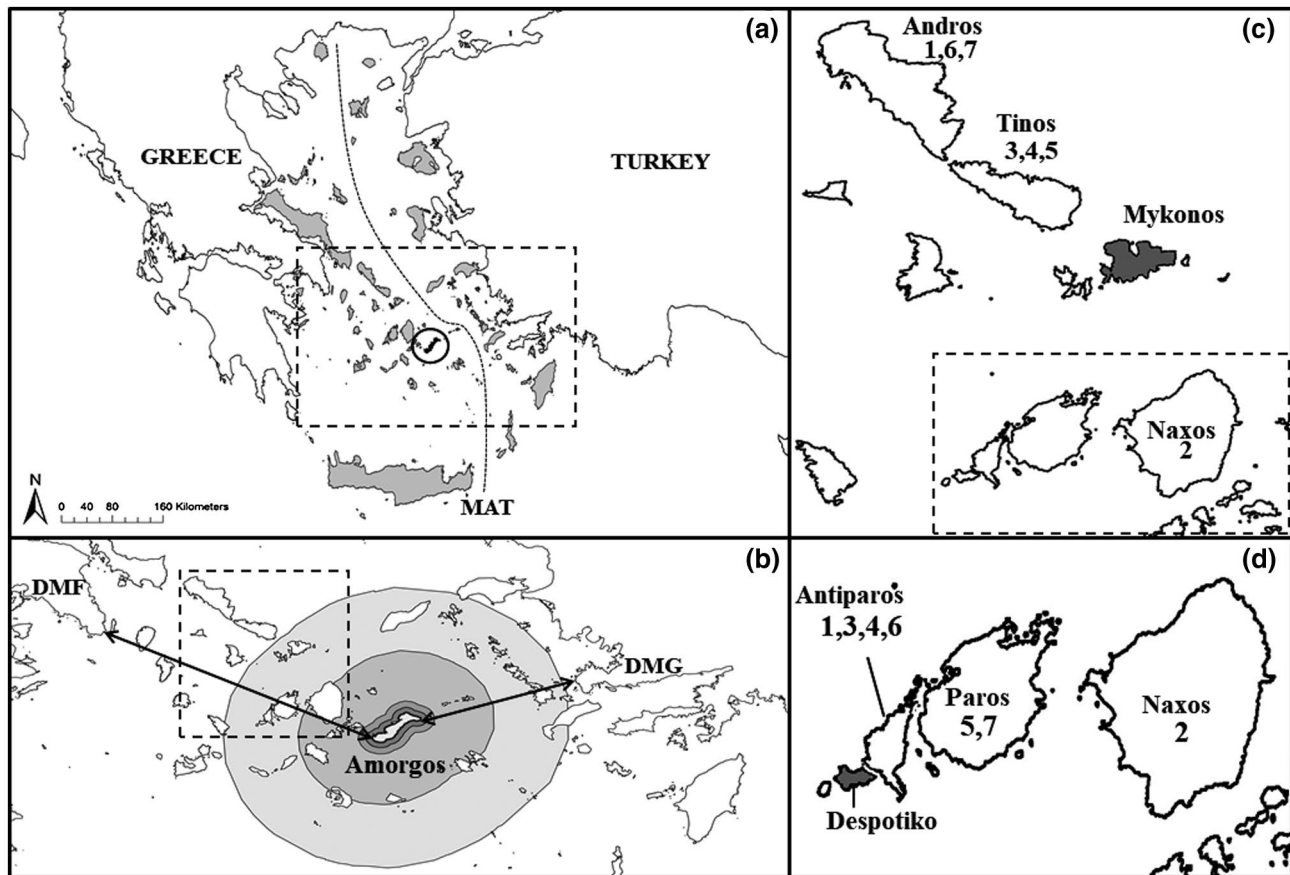


FIGURE 1 Schematic visualization of the different source land masses from which isolation indices have been calculated in this study, exemplified by real cases. Abbreviations: DMG = distance to the geographically nearest mainland; DMF = distance to the nearest mainland with similar fauna; MAT = Mid Aegean Trench (see main text). Numbers in panels c and d correspond to the codes of “D” (distance) and “T” (time) indices given in Table 1. Each panel zooms in to the dashed shape within the previous panel. (a) A map of the Aegean Sea showing the islands studied (in grey, except for Amorgos, which is encircled and marked in black) and the location of the MAT. (b) Amorgos Island surrounded by six buffers (in the grey gradient) illustrating indices B1–B6. Arrows indicate DMF and DMG, which are different for this island. (c,d) Focal islands Mykonos (c) and Despotiko (d), marked in dark grey, present an example of different spatial and temporal settings with regard to the neighbouring islands from which each “T” and “D” isolation index was calculated

found to affect species richness (e.g., Fattorini, 2002; Heaney, 1984; Sfenthourakis, 1996). Two recent studies, in which data from both oceanic and land bridge archipelagos were analysed, suggested that the effect of distance to the geographically nearest mainland on species richness is often overshadowed by the effects of intra-archipelago processes, driven by the spatial structure of islands (Ali & Meiri, 2019; Matthews, Rigal, Triantis, & Whittaker, 2019).

The explanatory power of temporal isolation indices (or “island age” parameters) has never been compared with that of spatial isolation indices for any group of organisms. Temporal isolation is hard to estimate, especially for land bridge islands. This might be the reason why it is studied less often than spatial isolation in general and why it is studied more often in oceanic islands (e.g., Ali & Meiri, 2019; Borges & Brown, 1999; Cameron et al., 2013) than in land bridge islands (but see e.g., Heaney, 1984; Wilcox, 1978).

Species richness is the most studied feature in island biogeography, but many other characteristics of insular animals are also thought to be affected by isolation (Lomolino, Riddle, Whittaker, & Brown, 2016; Losos & Ricklefs, 2009). Body size is arguably the

most studied phenotypic trait of animals, on islands and in general, and it is often thought to increase in small species and decrease in large species with increasing isolation (Itescu et al., 2018; Lomolino, 2005; Meiri, Dayan, & Simberloff, 2005). The logic behind this prediction is that increased isolation induces ecological conditions that drive animal size to an intermediate optimum (Lomolino, 2005). Increased spatial isolation means lower gene flow, and increased temporal isolation means a longer time for genetic differences to accumulate. More spatially or temporally isolated islands are therefore expected to show more extreme in situ evolution (Adler & Levins, 1994; Boback, 2003; Kisel & Barraclough, 2010; Pergams & Ashley, 2001). Isolation can also affect population-level characteristics. For example, because it is predicted to drive decreased species richness it is thought that highly isolated island populations enjoy reduced interspecific competition, which leads ultimately to increased population densities (Adler & Levins, 1994; Adler, Wilson, & Derosa, 1986; MacArthur, Diamond, & Karr, 1972; cf. Novosolov et al., 2016).

We investigated how the choice of which isolation index to study affects our inference of the impact of isolation on biological

TABLE 1 The isolation indices examined in this study

Isolation type	Spatial index code	Temporal index code	Response
Isolation from the geographically nearest mainland	DMG	TM	Richness and traits
Isolation from the nearest mainland with similar fauna	DMF		Richness and traits
Isolation from the nearest (larger) landmass (mainland or larger island) to which an island was last connected	D1	T1	Richness and traits
Isolation from the largest island in the cluster of the focal island	D2	T2	Richness and traits
Isolation from the nearest larger island	D3	T3	Richness and traits
Isolation from the nearest (reptile) species-richer landmass (mainland or larger island)	D4	T4	Lizard traits
Isolation from the nearest lizard predator-richer landmass (mainland or larger island)	D5	T5	Lizard traits
Isolation from the last reptile-richer landmass (mainland or larger island) to which an island was connected	-	T6	Lizard traits
Isolation from the last lizard predator-richer landmass (mainland or larger island) to which an island was connected	-	T7	Lizard traits
Landmass area within a buffer of 0.5 km radius around a focal island	B1	-	Richness and traits
Landmass area within a buffer of 1 km radius around a focal island	B2	-	Richness and traits
Landmass area within a buffer of 5 km radius around a focal island	B3	-	Richness and traits
Landmass area within a buffer of 10 km radius around a focal island	B4	-	Richness and traits
Landmass area within a buffer of 50 km radius around a focal island	B5	-	Richness and traits
Landmass area within a buffer of 100 km radius around a focal island	B6	-	Richness and traits

Note: Units are distance (in kilometres) for "D" (spatial) indices, area (in square kilometres) for "B" (spatial) indices and time (in years) for "T" (temporal) indices.

patterns on islands, and whether some indices consistently have a higher explanatory power across taxa. We examined community, population and individual characteristics to understand the extent to which patterns are general. We tested the most common prediction in the literature for each property we studied: (a) that species richness (a community-level property) declines with isolation (MacArthur & Wilson, 1963); (b) that population density (a population-level property) increases with isolation (Adler & Levins, 1994); and (c) that body size (an individual-level property) of small species is larger and that of large species is smaller on more isolated islands (Lomolino, 2005). We studied the fauna of the Aegean Archipelago (Greece), a system that, in recent decades, has been widely used in biogeographical studies of land bridge islands (Sfenthourakis, Pafilis, Parmakelis, Poulakakis, & Triantis, 2018). For species richness, we tested 15 isolation indices (11 spatial and four temporal) across 15

taxa. We tested the effects of 21 isolation indices (13 spatial and eight temporal) on body size across many populations of seven lizard species and the effects of the same 21 indices on the population density of three lizard species. We previously found that isolation has little effect on lizard body size (Itescu et al., 2018; Meiri, 2007) and now test whether our previous choice of isolation indices was the reason why the theory was refuted.

We hypothesized that:

1. Island area and the best isolation index would have similarly strong effects on patterns of insular fauna characteristics, as predicted by MacArthur and Wilson (1963, 1967).
2. The Aegean land bridge islands are often very young and were formed with an existing non-equilibrium fauna. If richness declines through extinction over time, temporal isolation would

have a stronger effect than spatial isolation on the properties of the fauna. Furthermore, we predicted that surrounding landmass area is more important than distances to other landmasses.

3. Most islands are closer to, and have been connected more recently to, nearby islands than to the mainland. Therefore, as recent results imply (Matthews et al., 2019), isolation from adjacent islands would be more strongly related to faunal characteristics than isolation from the mainland.

2 | MATERIALS AND METHODS

2.1 | Study system

The Aegean archipelago comprises c. 7,500 islands and islets that vary by several orders of magnitude in area and isolation (Sfenthourakis & Triantis, 2017). The geological and palaeozoological history of these islands is diverse and complex and has been thoroughly reviewed (Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014; Sfenthourakis et al., 2018; Sfenthourakis & Triantis, 2017; Simaiakis et al., 2017). Most of the Aegean islands are land bridge islands, which were connected either to Europe or to Asia Minor at various points in time, but a few have never been connected to any mainland. Some islands have been isolated since the Messinian salinity crisis (c. 5.3 Ma; Lymberakis & Poulakakis, 2010), whereas others became isolated more recently during the Pliocene and Pleistocene (Anastasakis & Dermitzakis, 1990). The majority of islands, however, became isolated only after the Last Glacial Maximum (LGM), mostly as a result of rising sea levels (Kapsimalis et al., 2009; Sakellariou & Galanidou, 2016; Simaiakis et al., 2017).

2.2 | Data collection

2.2.1 | Area and isolation indices

We obtained faunal data for 205 islands. We defined and estimated 21 isolation indices (13 spatial and eight temporal) for each island (Table 1). These represent a diversity of possible “source” landmasses. The indices we quantified include several previously studied ones and a few that we developed anew because we suspected that they could be important. We estimated three types of isolation indices: (1) temporal isolation indices (time, “T”) quantifying the time (in years) since separation between an island and a defined source landmass; (2) spatial isolation indices (distance, “D”) representing the minimal distances (in kilometres) between each focal island and a defined focal source landmass; and (3) spatial “buffer” (= B) isolation indices quantifying the amount of land area (in square kilometres) within a defined radius around the focal island. These three types reflect substantial variability in how they measure “isolation”, and we were able to calculate them with confidence for even the smallest islands. We focused on contemporary values of area and spatial isolation, because Weigelt, Steinbauer, Cabral, and Kreft (2016) showed that they were more important than past conditions (e.g., in late Quaternary) for total plant species richness on islands worldwide.

The potential source landmasses were mostly similar for “T” and “D” indices (Table 1). We calculated two alternative indices of distance from the mainland. The “geographically nearest mainland” is the part of the mainland from which the straight-line distance to the focal island is the shortest, regardless of their fauna. The “nearest mainland with similar fauna”, however, represents the nearest mainland region to which species pool the fauna of the focal island belongs. The fauna of the Aegean Sea islands is affected fundamentally by the Mid-Aegean Trench (MAT), a deep chasm in the Aegean Sea that opened 9–12 Ma (see Figure 1; Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014). Islands east of the MAT were usually connected to Asia Minor during periods of low sea levels, whereas most islands west of the MAT were connected to islands further west or even to mainland Europe. For some taxa (e.g., reptiles and amphibians; Lymberakis & Poulakakis, 2010), this palaeogeographical feature separates the islands east of the MAT from those to its west, biologically. In many taxa, islands on each side of the MAT have sets of species that are not found on islands on the other side, and only a few cases of species that have crossed this biogeographical barrier have been documented so far (Lymberakis & Poulakakis, 2010; Poulakakis et al., 2014). Geographically, however, some islands west of MAT (e.g., Amorgos, Fig. 1b) are closer to mainland Asia Minor which harbors the fauna characterizing islands east of MAT, than to Europe, to which their fauna is more similar. All islands east of the MAT are geographically closer to Asia Minor than to continental Europe. This discrepancy means that the potential mainland source for the fauna of some of the “western” islands is not necessarily the geographically nearest mainland. In terms of temporal isolation, however, this distinction is practically irrelevant. Continental Greece and Asia Minor have remained a continuous landmass ever since the end of the Messinian crisis (Lymberakis & Poulakakis, 2010) and therefore any temporal estimation of land mass disconnection (i.e., island isolation) from the mainland would be the same with regard to both regions.

An island cluster (with regard to the distance and temporal isolation from the largest island in a cluster: D2 and T2, respectively, in Table 1; Figure 1) was defined as all present-day islands that formed one continuous landmass during the LGM (i.e., c. 20,000 years ago; Figure 2). Indices relating a focal island to source landmasses with more potential competitor and predator species (D4, D5 and T4–T7 in Table 1; Figure 1) were studied for body size and population density of lizards only. They were based on data on potential competitors and predators provided by Itescu et al. (2018). We were unable to obtain enough reliable data to study them in other taxa.

We recorded the area of each island from official publications of the Hellenic Statistical Authority (2011) and, for small islets, using Google Maps tools (<https://www.daftlogic.com/projects-google-maps-area-calculator-tool.htm>). Distances between islands and source landmasses were calculated using Google Earth distance measurement tools. Disconnection times between each island and its source landmass were calculated by crossing fine-resolution bathymetric data (from the Hellenic Navy Hydrographic Service: www.hnhs.gr/geoindex/) with charts of sea level change since the

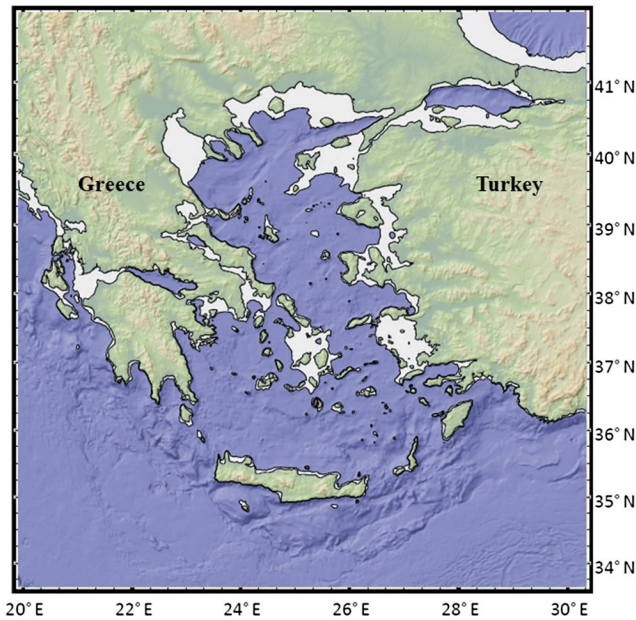


FIGURE 2 The Aegean Sea region at the Last Glacial Maximum (c. 20,000 years ago). The white areas were dry land at that time and today are under water. This map was created via GeoMapApp (<http://www.geomapapp.org/>; see Ryan et al., 2009) [Colour figure can be viewed at wileyonlinelibrary.com]

LGM (see Fofopoulou & Ives, 1999; Fofopoulou et al., 2011). This method has been implemented successfully in biological studies of land bridge archipelagos (e.g., Meik, Lawing, & Pires-daSilva, 2010; Wang et al., 2014).

Sea level rise since the LGM was not uniform across the Aegean region. Lambeck (1996) suggested that sea levels have risen more slowly towards the centre and south of the Aegean Sea. To refine the resolution of sea level time charts compared with previous estimates of this types in the Aegean region (e.g., Fofopoulou & Ives, 1999), we divided the Aegean Sea into 23 different sub-regions based on sea level rise data and maps (Dermitzakis, 1990; Kapsimalis et al., 2009; Lambeck, 1995, 1996; Perissoratis & Conispoliatis, 2003; Poulos, Ghionis, & Maroukian, 2009; Van Andel & Shackleton, 1982). We then calculated region-specific hypothesized time–depth charts (see Supporting Information Appendix S1, Table S1.1; Figure S1.1). These sub-regions represent areas that have presumably experienced different rates of sea level rise since the LGM, which means that a given present-day depth might have been flooded at different times in different regions (Simaikis et al., 2017). We recorded the estimated depths in each sub-region at several time periods as given in these publications. Then, for each pair of consecutive recorded time periods, we divided the number of years between them by the total change in depth during this time frame. The result was the hypothesized time at which sea level changed by each 1 m for that time frame.

The sub-regional charts were supplemented by island-specific estimations from the literature (see list of sources in Supporting Information Appendix S1) for islands that were isolated because of events such as earthquakes (e.g., Saria, Telendos). For islands that

were isolated before the LGM, we either used explicit estimations published in the literature or used a rough estimation of the minimal period for which the island was disconnected from any larger landmass, based on maps and data in the biogeographical literature (see Appendix 1). To estimate the disconnection time of islands from potential source landmasses, we recorded the maximal depth between each focal island–source landmass pair. We then extracted the matching hypothesized time period from the corresponding sub-regional time–depth chart.

Simaikis et al. (2017: see their appendix B, table S1) used a different model that also took into account the spatially non-uniform rise in Aegean Sea level since the LGM to estimate the timing of isolation of 31 Aegean islands. To examine whether the use of a different model (more straightforward, in our opinion) to estimate temporal isolation produced different results, we performed a sensitivity test in which we compared our island disconnection time estimations with those of Simaikis et al. (2017) for these 31 islands. Absolute estimations were older by 1,160 years, on average, in the study by Simaikis et al. (2017) than in our method. They were, however, very strongly correlated (Spearman's $\rho = 0.96$, $p < .001$, $n = 31$ islands). Simaikis et al. (2017) explicitly mentioned that they trusted the chronological order of the island separation events they found, which is practically similar to what we found, more than the specific calculated timing in years. Thus, we feel confident that the choice of estimation model has not affected our inference, despite the slight difference in timing estimations.

To calculate the “B” indices (i.e., surrounding land area) we used the QGIS v.3.6.3-Noosa software and followed the procedure described by Weigelt and Kreft (2013). Given that studies showed that the effect of surrounding land area on species richness varies across spatial scales (Diver, 2008; Weigelt & Kreft, 2013), we applied the “buffer” tool, with six different radii for each focal island, on azimuthal equidistant projected maps: 0.5, 1, 5, 10, 50 and 100 km (B1–B6, in that order). The buffers were drawn around and relative to the circumference of the focal island. We then calculated the land area locked within each buffer and subtracted the area of the focal island from the total area. This gave us six “B” indices, varying in the geographical range they cover, for each focal island (for values of all 21 indices for each island, see Supporting Information Appendix S2, Table S2.1).

2.2.2 | Species richness and lizard body size

We recorded data (see Supporting Information Appendix S2, Table S2.1) on species richness of mammals (Masseti, 2012), breeding land birds (Simaikis et al., 2012), reptiles (our own data; see below), land snails (Triantis, Vardinoyannis, & Mylonas, 2008; Welter-Schultes & Williams, 1999), centipedes (Simaikis, Minelli, & Mylonas, 2005), non-halophilous isopods (Sfenthourakis, 1996; Sfenthourakis & Triantis, 2009), butterflies (Dennis, Shreeve, Olivier, & Coutsis, 2000), darkling beetles (Tenebrionidae; Anastasiou, Papadopoulou, & Trichas, 2018; Fattorini, 2002;

Trichas, Lagkis, Triantis, Poulakakis, & Chatzaki, 2008), orthopterans (Willemse, Kleukers, & Odé, 2018) and *Merodon* flies (Vujić et al., 2016). These taxa represent a diversity of life-forms and dispersal abilities. We analysed only islands that had data for at least one taxon and had at least one species of that taxon. To examine whether patterns are consistent across taxonomic levels, we also analysed species richness of the following, well-sampled and species-rich, subsets: rodents, snakes, lizards, bush-cricket and grasshoppers.

We recorded all known distribution records of Aegean reptiles from > 350 publications and six museum catalogues [Zoologische Staatssammlung München, Zoologisches Forschungsmuseum Alexander Koenig (Bonn), Museum für Naturkunde Berlin, Naturhistorisches Museum Vienna, Natural History Museum of Crete and Museum of Comparative Zoology at Harvard University; see Itescu, 2017]. To that, we added our own field observations (e.g., Itescu, Jamison, et al., 2017; Itescu, Schwarz, Moses, Pafilis, & Meiri, 2016; Itescu, Slavenko, Schwarz, Meiri, & Pafilis, 2016).

Mean body size [snout-vent length (SVL)] data for lizard species (*Ablepharus kitaibelii*, *Hemidactylus turcicus*, *Lacerta trilineata*, *Mediodactylus kotschyi*, *Mediodactylus oertzeni*, *Ophisops elegans* and *Podarcis erhardii*) were taken from Itescu et al. (2018; supplemented with a few minor updates). These represent our measurements in museums and in the field, and literature data. We included only species for which we had mean body size data from ≥ 10 islands, for which we could calculate all 21 isolation indices. Fourteen island populations that were classified as *M. kotschyi* by Itescu et al. (2018) were reclassified here as *M. oertzeni*, following a recent update to their taxonomy (Kotsakiozi et al., 2018), and were thus analysed separately.

We estimated population density in the field by applying species-specific methods. To estimate relative population densities of *M. kotschyi* across 40 islands, we calculated, for each population, the mean number of geckos one of us (Y.I.) found per hour of search in clear sky conditions during peak activity hours (Buckley & Roughgarden, 2005, 2006; Itescu, Schwarz, Meiri, & Pafilis, 2017). We estimated relative densities of *P. erhardii* from 55 islands through straight-line transects performed by three people simultaneously walking 100 m in parallel 10 m from each other during the peak activity time of the lizards and counting lizards seen or heard 1.5 m from each side. The three counts were then averaged. This was performed twice at a 48 hr interval and averaged. This method has been used successfully to estimate *Podarcis* densities (Brock, Bednekoff, Pafilis, & Foufopoulos, 2015; Donihue, Brock, Foufopoulos, & Herrel, 2016; Pérez-Mellado et al., 2008). For *H. turcicus* ($n = 21$ islands), we estimated relative densities by averaging the number of geckos found by one searching person during a full day (both during the day and at night; Itescu, Schwarz, et al., 2017).

2.3 | Statistical analyses

We evaluated the statistical significance of results in the present study at the $\alpha = .005$ level. This decision followed recent calls for a

more conservative approach in using statistical significance for testing hypotheses (Benjamin et al., 2018; Johnson, 2013). It was also required here because all our analyses included multiple comparisons and repeated tests. Nevertheless, given that $\alpha = .05$ is still commonly used to determine statistical significance, we present all results with a p -value of $.005 < p < .05$ either in the main text or in the Supporting Information (Appendix S3).

To analyse the data adequately, we \log_{10} -transformed the species richness of all taxa, the mean body size of *P. erhardii* (the residual distribution of other species was normal without transformation), the population density of *P. erhardii* and *H. turcicus*, and all predictor variables, because a Shapiro–Wilk normality test indicated that they differed significantly from normality (at $\alpha = .005$). This procedure normalized the residuals of the regression tests we performed to a large extent. Landmass area ≤ 10 km radius around certain islands (B1–B4 indices) was zero. To be able to \log_{10} -transform these indices, we converted these zeros to 0.0000001. This made them transformable but still smaller than the smallest value for any island in any of these indices.

We first regressed each response variable (\log_{10} -transformed if necessary) against \log_{10} -transformed island area and included island area as a covariate in all analyses where it proved significant (i.e., species richness for all taxa and population density of *P. erhardii*). Area was excluded from analyses of mean body size of all species and population density analyses of *H. turcicus* and *M. kotschyi*. We tested for collinearity between each isolation index and island area (using the HH package in R; Heiberger, 2009). No variance inflation factors were higher than the conservative cut-off value of four (O'Brien, 2007).

To test how each isolation index affects each property in each taxon, we performed a series of ordinary least squares regression tests, with species richness, mean body size and population density as the response variables. We used a single isolation index at a time as the predictor variable, and added island area as a covariate when necessary. We also tested for two-way interactions between each isolation index and island area, to investigate whether large islands respond to isolation in a different manner to small islands, like the reported pattern in plants (Weigelt & Krefl, 2013).

To test which isolation indices explain most of the variance in species richness of each taxon, we used the “calc.relimp” function in the “relaimpo” R package (Grömping, 2006), which calculated the partial R^2 for isolation in each model. We did not use information criteria, such as the Akaike information criterion (AIC), for model selection because it is not rare for the AIC to select models that statistically reflect no effect of the predictor variable on the response variable (MacNally, Duncan, Thomson, & Yen, 2018; see also Itescu et al., 2018). Another reason was that the AIC method scores full models (i.e., area and isolation, not only isolation) and therefore might score models in which island area explains more variance better, although isolation explains less variation in them than in alternative models with higher AIC scores. This would not allow us to compare the explanatory contribution of different isolation indices, which is what we were interested

in. Thus, we preferred to rank the statistically meaningful models (those with $p \leq .005$) by the partial R^2 explained by the tested isolation index. We think this is a more informative procedure with regard to the aim of this study. We applied a similar selection procedure for mean body size and population density models (comparing the model's total R^2 for univariate isolation models).

To examine which isolation indices were superior overall (we were able to test this only for species richness) and whether they were temporal or spatial indices, we used a DerSimonian–Laird random-effect meta-analysis of correlation coefficients of all studied taxa. Here, the square root of the partial R^2 scores of each isolation index were treated as the effect sizes, which we treated as random effects. This procedure calculates the mean relationship between isolation and species richness across “studies” (in our case, taxa) for each “treatment” (i.e., isolation index) (see Laliberté et al., 2010). Thus, it enabled us to determine which isolation index had the strongest effect across taxa. We performed the meta-analysis with the function “metacor.DSL” in the “metacor” R package (Laliberté, 2011).

3 | RESULTS

3.1 | Species richness

Isolation was a statistically significant predictor of species richness in 10 of 15 taxa. In the remaining five taxa (Tenebrionids, *Merodon* flies and the three orthopteran groups), no isolation index significantly affected species richness. The isolation index with the highest explanatory power varied across taxa (Table 2; Figure 3), but in all 10 taxa the spatial indices were superior to the temporal ones. The distance to the nearest mainland with similar fauna (DMF) explained more variance than any other index in four groups, land area within a buffer of 100 km radius (B6) in two groups (all reptiles and lizards alone), and the distance to the geographically nearest mainland (DMG), land area within a buffer of 0.5 km radius (B1) and the distance to the nearest larger landmass (D3) in one group each (land snails, isopods and mammals, respectively). For butterflies, DMF and DMG were identical and explained more variance than any other index. Distance to the nearest mainland with similar fauna (DMF) and to the geographically nearest mainland (DMG) were the most frequently significant indices (each in seven taxa, including butterflies), followed by the most frequently significant temporal index, which was the time of isolation from the mainland (TM; in six groups), and land area within buffers of 50 and 100 km radii (B5 and B6, respectively; each in five groups). These five indices, which are directly related to the mainland (DMF, DMG and TM) or largely (B5 and B6, in which the buffers include parts of the mainland for the majority of islands), were the top three for all taxa except mammals and isopods. Of all indices, land area within buffers of 5 and 10 km radii (B3 and B4, respectively) were the least important. They were not significant for any group (all models with p -values of $.005 < p < .05$ are presented in Supporting Information Appendix S3, Table S3.1). Only four out of 224 potential interaction terms between isolation indices and island area were statistically significant. Four additional interaction terms

were marginally non-significant (i.e., had $.005 < p < .05$; Supporting Information Appendix S3, Table S3.2).

Island area was strongly and positively correlated with species richness in all taxa. Area alone explained 31.5–85.3% of the variance in species richness across taxa (see Supporting Information Appendix S3, Table S3.2). When area and isolation were tested together, the partial R^2 for the most important isolation index in each group ranged between 10.4 and 27.8%, whereas island area explained 72.2–89.6% of this variance (Table 2), except for butterflies, for which the partial R^2 for isolation was 50.9% (for the distance from the mainland; see comment in Table 2). This was the only case, across 224 models, in which isolation explained more variance than area.

In the meta-analysis (Table 3; Supporting Information Appendix S3, Figure S3.1), island area alone explained 66.4% of the variance in species richness across all studied taxa. The isolation index with overall highest partial R^2 was the distance to the nearest mainland with similar fauna (DMF; 14.7%). The only significant temporal index was the time since isolation from the mainland (TM). Eight indices were not significant overall (land area within a buffer of 0.5 km radius, B1, was marginally non-significant). All significant indices showed the same expected trend: a negative association between isolation and species richness.

3.2 | Body size and population density

Only one of 147 models for mean body size was statistically significant: a positive relationship between mean body size of *A. kitaibelii* and the distance from the largest island in the cluster of the focal island (D2). For the other six species, the effect of the strongest isolation index on mean body size was borderline non-significant ($.005 < p < .061$). Nonetheless, it is noteworthy that, across these six species, five different indices were chosen, and these represent all three tested isolation types (D, B and T) and the two main source types (i.e., the mainland or adjacent landmasses; Table 4). All the best models showed that body size increases, albeit not significantly, with isolation (Table 4; Figure 3).

No isolation index significantly predicted population density in any species (Table 4). In *P. erhardii* (only), island area was negatively associated with population density. Even under the permissive threshold for statistical significance ($p < .05$), none of the 21 indices we tested was correlated with the population density of *H. turcicus*, one had a negative effect in *M. kotschy*, and three had a positive effect in *P. erhardii* (Table 4). Under this threshold, *M. kotschy* density increased with landmass area within a buffer of 5 km radius around a focal island (B3). The best (but still not very good) index for *P. erhardii* was distance from the nearest (larger) landmass to which an island was last connected (D1).

4 | DISCUSSION

We found that isolation is negatively correlated with richness in most taxa. In contrast, isolation seems to affect neither lizard body

TABLE 2 Regression statistics of \log_{10} -transformed species richness as a function of different isolation indices of studied taxa

Taxon	Model	Slope	Total R^2	Partial R^2 area (%)	Partial R^2 isolation (%)	p	n
Mammals	D3	-0.088	.768	89.6	10.4	.001	116
	D1	-0.080	.771	92.2	7.8	<.001	
	B2	0.022	.763	94.8	5.2	.003	
	T1	-0.054	.762	97.6	2.4	.005	
Rodents	DMF	-0.097	.719	73.7	26.3	<.001	102
	DMG	-0.094	.712	75.4	24.6	<.001	
	B6	0.169	.708	79.7	20.3	<.001	
	TM	-0.048	.702	83.7	16.2	<.001	
Land birds	DMF	-0.147	.857	76.2	23.8	<.001	65
	DMG	-0.149	.855	78.0	22.0	.001	
	TM	-0.067	.860	83.0	17.0	<.001	
Reptiles	B6	0.194	.718	85.3	14.7	<.001	205
	DMF	-0.092	.722	85.9	14.1	<.001	
	DMG	-0.082	.717	88.4	11.4	.004	
	TM	-0.054	.723	89.0	11.0	<.001	
	B5	0.129	.720	91.6	8.4	<.001	
	B2	0.022	.715	97.0	3.0	<.001	
Lizards	B6	0.119	.658	85.7	14.3	.001	202
	DMF	-0.053	.664	86.7	13.3	.005	
	B5	0.088	.663	90.9	9.1	<.001	
Snakes	DMF	-0.153	.695	72.2	27.8	<.001	90
	DMG	-0.151	.691	73.5	26.5	<.001	
	B6	0.291	.691	77.6	22.4	<.001	
	TM	-0.168	.670	85.3	14.7	.001	
	B5	0.224	.675	90.3	9.7	<.001	
Butterflies	DM ^a	-0.216	.840	49.1	50.9	<.001	28
	B6	0.344	.790	51.8	48.2	<.001	
	TM	-0.100	.731	54.0	46.0	<.001	
	D2	-0.255	.762	56.3	43.7	<.001	
	D1	-0.217	.756	58.8	41.2	<.001	
	B5	0.276	.723	59.5	40.5	<.001	
	D3	-0.251	.740	63.6	36.4	<.001	
	T3	-0.093	.601	66.7	33.3	<.001	
	T2	-0.086	.539	71.3	28.7	.002	
	T1	-0.086	.539	71.4	28.6	.002	
Centipedes	DMF	-0.167	.655	73.2	26.8	<.001	55
	DMG	-0.182	.664	73.9	26.1	<.001	
	TM	-0.098	.613	81.2	18.8	<.001	
Land snails	DMG	-0.122	.781	88.7	11.3	.002	85
	B5	-0.133	.781	96.3	3.7	.002	
Isopods	B1	0.018	.875	86.2	13.8	.001	68
	B2	0.021	.879	94.4	5.6	<.001	
Merodon flies	None						27
Tenebrionid beetles	None						57

(Continues)

TABLE 2 (Continued)

Taxon	Model	Slope	Total R ²	Partial R ² area (%)	Partial R ² isolation (%)	<i>p</i>	<i>n</i>
Orthopterans	None						65
Bush-crickets	None						52
Grasshoppers	None						60

Note: Log₁₀-transformed island area was a covariate in all models. Only statistically significant models ($p \leq .005$) are shown. Partial R² area and partial R² isolation are the relative contribution of each variable to the total R². The highest partial R² isolation in each taxon is in bold.

^aIn butterflies, the distance to the nearest mainland with similar fauna (DMF) and distance to the geographically nearest mainland (DMG) were identical and were referred to as DM.

size nor population density. We have demonstrated that isolation indices are not equally important across taxa, and sometimes even across taxonomic levels within a single taxon, for the same focal characteristic. We found no support for the hypothesis that area and isolation explain substantial and equal portions of the variance in insular fauna characteristics. Area explained substantially more of the variance in species richness than any isolation index in 223 out of 224 models. For body size and population density, neither area nor isolation explained a substantial portion of the variance.

These results also sharply refute our second hypothesis, that temporal isolation is more important than spatial isolation for land bridge island fauna. Temporal isolation indices seem to be the least influential of the studied metrics, whereas distance-based indices seem to be the most influential. Additionally, indices that are directly related to the mainland seem to be more important in predicting the species richness of most studied taxa, refuting our third hypothesis. Thus, overall, the results do not support any of our three hypotheses.

Isolation is expected to be negatively correlated with species richness (MacArthur & Wilson, 1963, 1967; Whittaker et al., 2008). This seems to be true for two-thirds of the taxa on the Aegean islands. Notably, all five taxa in which isolation had no impact are insect groups. The simplest explanation for the results of these five groups is that they are not constrained by isolation. Another possibility is that the current published data for species richness of these groups is too incomplete to be reliable, owing to problems such as unequal sampling efforts across islands and taxonomic uncertainties. These are likely in small animals. A non-mutually exclusive alternative is that the range of isolation in the set of islands we analysed for these taxa (which differed across taxa) was too small for isolation to play a major role in this system. We note that additional factors, such as the prevalence and direction of winds and sea currents, are especially important for insects. These factors, however, cannot explain our findings for butterflies and isopods. Weigelt and Kreft (2013) found that these factors affect plant species richness. In some taxa for which we found an association between isolation and species richness, studies conducted in other regions found no such relationship (e.g., SE Asian and Australian mammals: Burbidge, Williams, & Abbott, 1997; Heaney, 1984; British butterflies: Dennis & Shreeve, 1997; Brazilian snakes: Portillo et al., 2019). This could be a consequence of these studies not including the best indices. Alternatively, we suggest that the impact of isolation might depend on the spatial structure of a focal archipelago: patterns may be different between

archipelagos close to the mainland and those far from it (see e.g., Ås, 1984; Dennis & Shreeve, 1997; Foufopoulos & Mayer, 2007; Nilsson, Bengtsson, & Ås, 1988). This seems plausible, especially in cases where the same index shows inconsistent patterns across regions for the same taxon. For example, the distance from the geographically nearest mainland did not affect the richness of snakes in Brazilian Atlantic Forest coastal islands (Portillo et al., 2019) but had a significant negative effect on snake richness in the Aegean Sea islands and explained 18.3% of its variance (present study, Table 2).

Our results for animals are also inconsistent with those of Weigelt and Kreft (2013), who found that worldwide species richness of plants on large islands was less affected by isolation than on small ones. Biogeographical patterns are often dissimilar between plants and animals (Currie, 1991; Hawkins et al., 2003); therefore, this result is not surprising. Nevertheless, it could also be a matter of the scale of study; perhaps, interactions between island area and isolation are easier to detect at the global scale.

The influence of isolation (both spatial and temporal) on species richness was much weaker than that of island area, which affected all our studied taxa strongly and positively. This is in line with the results of a meta-analysis by Watling and Donnelly (2006), who showed that 92% of studies find a significant species–area relationship, but only 33% find a significant species–isolation relationship. Our results also agree with those of Matthews et al. (2019), who found that isolation (measured as the distance from the geographically nearest mainland) affected species richness much more weakly than did area, across multiple archipelagos. The relative weakness of isolation, however, stands in sharp contrast to the predictions of the dynamic theory of island biogeography (MacArthur & Wilson, 1963, 1967), where it was portrayed to have as strong effect as island area. Here, we demonstrated that the superior explanatory power of island area compared with that of isolation is consistent regardless of which isolation index is tested. Butterflies are the only group for which we found an index of isolation (but only one index, the distance from the mainland) that had an equally strong influence on species richness as island area (c. 50% of the explained variance each).

The relative weakness of isolation has several non-mutually exclusive potential explanations. One possibility is that present-day species–isolation relationships are severely obscured by anthropogenic activity (Helmus, Mahler, & Losos, 2014), which has been ongoing for several thousand years in our study system, as described

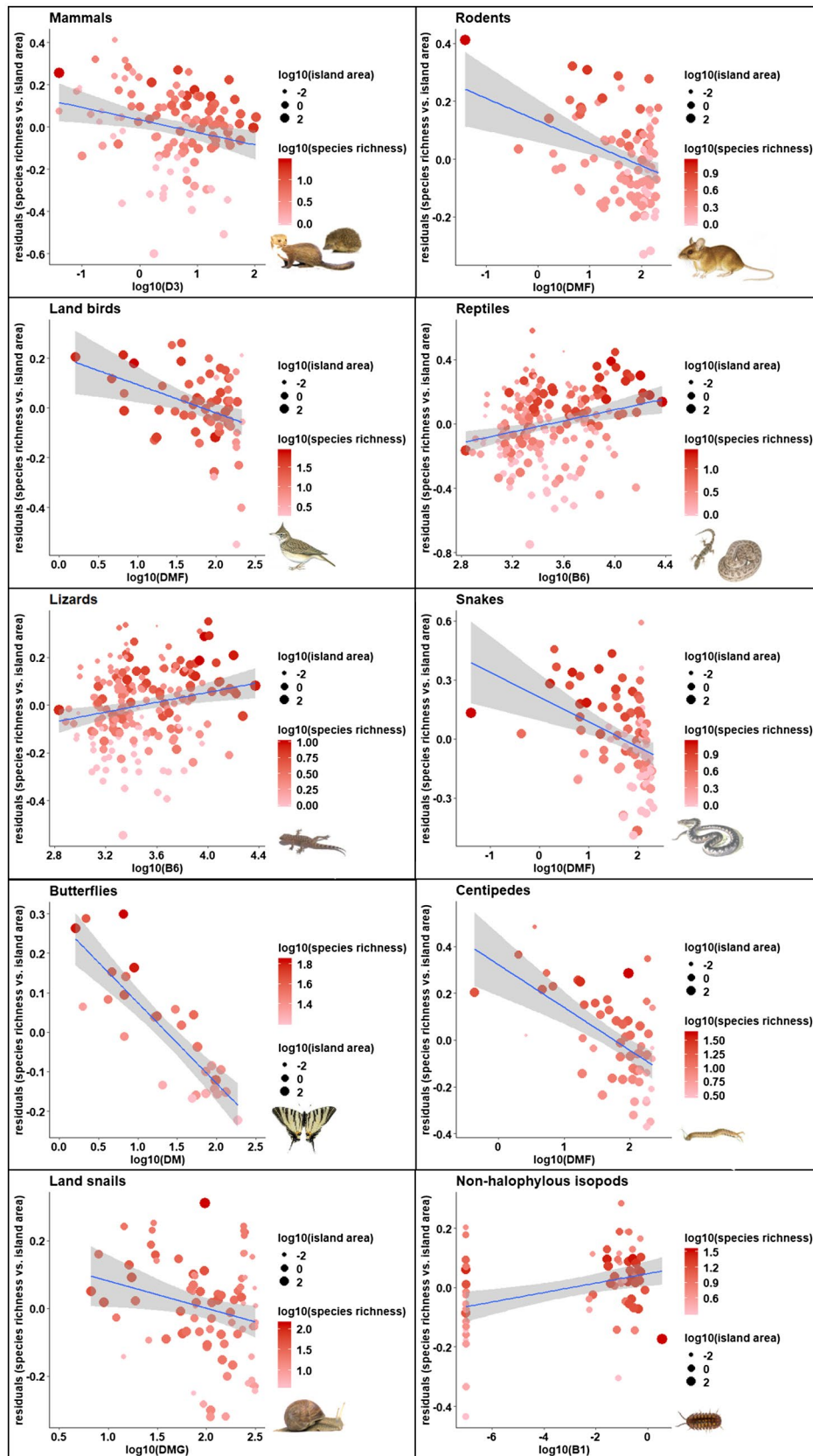


FIGURE 3 Scatter plots describing the relationship between the most important isolation index and species richness (controlled for island area) in the 10 taxa in which we found a statistically significant relationship. The area and species richness of islands (both \log_{10} -transformed) are visualized by the size and the colour of points, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of a meta-analysis for the effect of area and isolation on species richness across all 15 taxa

Index	Mean <i>r</i>	Range (<i>r</i>)	<i>p</i>
Area	.815	.775 to .849	<.001
DMF	-.383	-.474 to -.284	<.001
DMG	-.370	-.464 to -.270	<.001
B6	.232	.146 to .316	<.001
D3	-.219	-.375 to -.052	.005
D1	-.184	-.338 to -.021	.014
TM	-.174	-.331 to -.007	.002
B5	.148	.062 to .232	<.001
B1	.113	.021 to .204	.007
B2	.095	.040 to .150	<.001
B4	.048	-.008 to .103	.047
B3	.036	-.020 to .092	.101
D2	.034	-.145 to .210	.356
T3	-.020	-.184 to .145	.408
T1	-.010	-.170 to .150	.451
T2	.004	-.153 to .162	.478

Note: For isolation indices, the analysed values are of partial R^2 (from bivariate models with area), but for area they are derived from univariate models. Significant indices ($p \leq .005$) are in bold. Variables are presented in descending order of their mean explanatory power.

by the famous Greek classical poet, Homer (Lattimore, 1951). This activity has impacted local ecosystems through land-use change and species introductions. In some cases, it is not clear whether a newly discovered species is a “missed” native or a recent introduction (e.g., Itescu, Slavenko, et al., 2016), and this might have an impact on species richness counts. A second possibility is that the variation in island area is far larger than that of spatial isolation. In our system, island area spans six orders of magnitude, whereas distance-based isolation indices spans four at most. This may hamper finding strong relationships between species richness and isolation (Watling & Donnelly, 2006). Another possibility is that the rapid rates of area change in the region (as a result of changes in sea level) have not yet allowed islands to reach equilibrium (Simaiakis et al., 2017). Be that as it may, our results strongly imply that the length of the isolation period is a weak force, and thus explanations based on insufficient time for reaching equilibrium (assuming that equilibrium exists) are highly unlikely, even in this land bridge island-dominated system.

Surprisingly, we found that land bridge island faunas are generally affected more strongly by spatial isolation than by temporal isolation. This contrasts with conclusions of previous studies (Case, 1975; Fofopoulos & Ives, 1999) and with our own predictions. Distance-based indices performed consistently better than indices of surrounding land area (in contrast to patterns found in plants; Diver, 2008; Weigelt & Krefl, 2013), which in turn were superior to temporal indices. This pattern might be a consequence of very rapid changes in the Aegean insular fauna after isolation. Gibson et al. (2013) demonstrated that extinction may occur very quickly after an island disconnects from its “mother” landmass, and the system

enters a new state within a very short time period (a few hundreds of years or less; see also Burkey, 1995). This has direct implications for species richness, and a potential indirect influence on body size and population density, by reducing the numbers of interspecific competitors and predators (MacArthur et al., 1972; cf. Meiri et al., 2014). Studies demonstrated that phenotypic characteristics, such as body size, might indeed change drastically in short time-scales after isolation (Aubret, 2015; Lister, 1989). Other factors can also induce rapid microevolutionary changes on islands: extreme weather events, such as storms (e.g., Donihue et al., 2018), larger-scale climatic oscillations, such as droughts or rainy years (Grant et al., 2017), and anthropogenic activities, such as introduction of predators or competitors, land use changes, etc. (e.g., Jackson, Fuller, & Campbell, 2004; Littleford-Colquhoun, Clemente, Whiting, Ortiz-Barrientos, & Frère, 2017; Stuart et al., 2014). Under these scenarios, being isolated for 10,000 or 100,000 years makes no difference if richness has reached a plateau, or a phenotypic trait has reached an “optimal” state, after only a few hundreds of years. The vast majority of the islands we studied have been separate entities for at least a few thousand years. In contrast, spatial isolation affects species richness and evolutionary changes by controlling species and individual (i.e., gene) flow into islands, which is independent of any biological process occurring on the island.

No isolation index we tested, including the distance to the geographically nearest mainland (DMG), which is the most commonly examined index in the literature, was universally superior to other indices. Moreover, no index predicted species richness, mean body size or population density similarly well in all taxa. The relative importance of isolation indices and their magnitude of effect on species richness were inconsistent even across phylogenetically close taxa, taxonomic levels within certain taxa (e.g., rodents compared with all mammals, snakes compared with all reptiles), or taxa that presumably hold similar dispersal abilities. In the case of flying insects, for example, butterfly richness declined significantly as isolation increased, regardless of index, whereas *Merodon* fly richness did not respond significantly to any isolation index. Likewise, centipedes and isopods, both of which are ground-dwelling arthropod taxa, showed different patterns (Table 2).

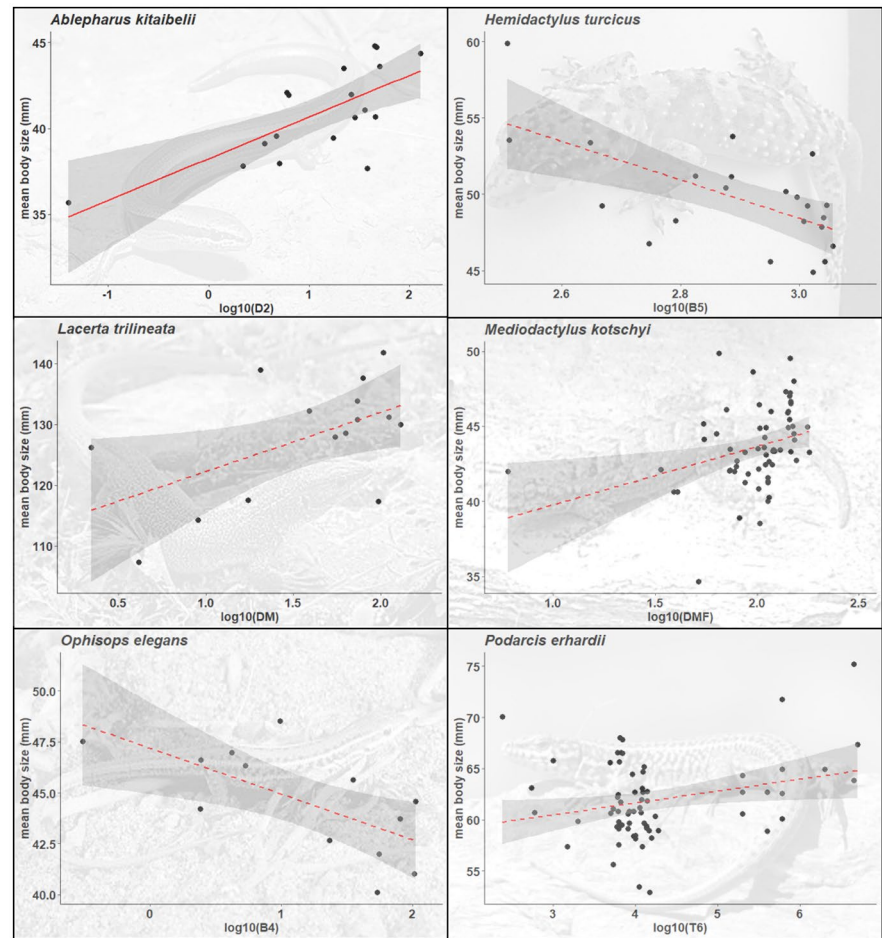
The interpretation of the effects of isolation on mean body size is complicated. Isolation has little effect on body size in lizards, consistent with previous findings (Itescu et al., 2018; Meiri, 2007). We tested 21 different indices on seven species (i.e., 147 models), and only one of them emerged as significant at $\alpha = .005$. This suggests that isolation and body size are genuinely not related and that this pattern is not a result of disregarding important isolation indices. However, researchers working with $p < .05$ as their threshold for statistical significance might interpret the results differently, because for each lizard species there was at least one significant result (at $p = .061$ for *M. oertzeni*, $.005 < p < .05$ for all other species). The less conservative thresholds suggest that size is larger on more isolated islands. Yet, even in this case, the prediction that body size reacts to isolation as a function of whether it is small or large (Lomolino, 2005) is not supported. The size of the smallest species in our dataset

TABLE 4 Model statistics for lizard mean body size (snout-vent length) and population density as a function of isolation

Attribute	Species	Model	Slope	Total R ²	Partial R ² (%)	p	n
Mean snout-vent length	<i>Ablepharus kitaibelii</i>	D2	2.426	.591	-	<.001	18
		DMF	1.787	.386	-	.006	
		DMG	1.620	.330	-	.013	
	<i>Hemidactylus turcicus</i>	B5	-7.331	.220	-	.021	24
		DM	9.734	.303	-	.033	15
		DMF	3.889	.104	-	.010	62
	<i>Lacerta trilineata</i>	DMG	3.114	.097	-	.014	
		B6	-3.426	.073	-	.034	
		None	-	-	-	-	14
	<i>Mediodactylus oertzeni</i>	B4	-2.248	.455	-	.011	13
		D3	2.711	.351	-	.033	
		D1	2.365	.344	-	.035	
	<i>Podarcis erhardii</i>	T1	1.604	.329	-	.040	
		T6	0.008	.069	-	.031	67
		D4	<0.001	.066	-	.035	
		D5	<0.001	.063	-	.041	
		None	-	-	-	-	21
	Population density	<i>Hemidactylus turcicus</i>	None	-	-	-	-
B3			0.597	.110	-	.037	40
<i>Mediodactylus kotschyi</i>		Area	-0.128	.220	-	<.001	55
		Area	-0.197	.279	84.4	<.001	
<i>Podarcis erhardii</i>		D1	0.133	15.6	15.6	.044	
		Area	-0.184	.297	86.6	<.001	
		T3	0.160	13.4	13.4	.020	
Area		Area	-0.161	.281	89.0	<.001	
		B3	-0.150	11.0	11.0	.039	

Note: Only models with $p < .05$ are presented. Statistically significant models ($p \leq .005$) are in bold. All predictor variables, mean body size of *P. erhardii*, and population density of *P. erhardii* and *H. turcicus* were \log_{10} -transformed. n is the number of islands. In *L. trilineata*, the distance to the nearest mainland with similar fauna (DMF) and distance to the geographically nearest mainland (DMG) were identical and were referred to as DM. Island area was statistically significant and included as a covariate only for population density of *P. erhardii*.

FIGURE 4 Scatter plots describing the relationship between the isolation index with lowest p -value (for the six species in which $p < .05$; a different index in each case, as shown on the x axis labels) and mean body size. Trend lines illustrate statistical significance levels: continuous lines are for $p < .005$; dashed lines are for $.005 < p < .05$. Isolation is stronger when “D” and “T” indices are larger but “B” indices are smaller (thus all six trends here are essentially in the same direction) [Colour figure can be viewed at wileyonlinelibrary.com]



(*A. kitaibelii*) increased with isolation, as expected, but so did the size of the largest species (*L. trilineata*), which was predicted to decrease. At the same time, it is clear that had we tested (using an α of .05) only one index for all species, our conclusions would be different for alternative indices we tested. For example, testing only the distance to the geographically closest mainland (DMG), we would have concluded that three of the seven species are affected by isolation. Using isolation indices such as land area within relatively large buffers (e.g., B5 or B6) would show that only one species is affected by isolation, and testing the time of isolation from the mainland (TM) would have driven us to conclude that isolation is not related to mean body size in lizards at all.

The indices that are directly related to the mainland (distance to the nearest mainland with similar fauna, distance to the geographically nearest mainland and time of isolation from the mainland) explained species richness better than indices of isolation from other islands. This stands in contrast to the finding of Matthews et al. (2019) and might mean that species richness in the Aegean Sea islands reflects a relaxation process with minimal contribution of between-island dispersal generating new colonizers (Foufopoulos & Ives, 1999). Out of the buffer (type B) indices, the largest radii (up to 50–100 km around islands) had the strongest impact on species richness of most taxa. Considering that, for most of the study islands, the mainland is well within buffers with such radii, we think that this is further evidence

emphasizing the importance of the mainland to species richness. Moreover, this result is largely in line with findings (for plants) that in a small-scale system, such as an archipelago in Lake Ontario (Diver, 2008), the amount of land area in the very close surroundings (within 0.25 km around islands) is most important, whereas at a global scale, area within 100–10,000 km around islands is most influential (Weigelt & Kreft, 2013). The Aegean archipelago is of an intermediate scale compared with the two other aforementioned systems, and thus the higher explanatory power of the indices quantifying land area within buffers of 50–100 km around islands fits this trend.

We conclude that the choice of which definition of isolation to use for studying insular biota can affect our inference of the magnitude of impact of isolation on biological patterns. Several relatively clear patterns emerge from our results for species richness. First, the effect of isolation on species richness is far weaker than that of island area, regardless of which index is tested. Second, spatial isolation indices tend to explain more variance than temporal indices. Third, isolation from the mainland explains more variance of species richness than isolation from adjacent islands. Finally, although the distance to the geographically nearest mainland (DMG) is the most straightforward index of isolation to measure, it is not necessarily the most informative. Although this index is not a bad choice per se, for many taxa it was inferior to other indices, including to its refined version, the distance to the nearest mainland with similar fauna (DMF). For body size,

it was not significant in most cases, and some indices performed better (but still poorly). Therefore, we recommend that the distance to the geographically nearest mainland should not be chosen automatically as the only index of isolation in a study, regardless of the attributes, taxa and system studied. We agree with Diver (2008) and Weigelt and Kreft (2013) that the impact of isolation on characteristics of insular biota could be modelled and understood better by studying additional indices. We think that the best way to approach this issue is to study several types of isolation indices simultaneously (e.g., the three we studied here and others that are based on, for example, climatic parameters or oceanographic parameters), to be able to encompass the complexity of this factor and its influence on insular biota. Despite the relative prominence of spatial isolation and mainland-related indices in this study, compared with other indices, we acknowledge the possibility that in other study systems the patterns might well be different. Simultaneous multi-index testing is essential to understand whether the weaker effects of temporal isolation are the norm across island systems and taxa.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

AUTHOR CONTRIBUTIONS

Y.I. conceived the idea, performed the analyses and led the writing; all authors collected the data and contributed to the writing process.

DATA AVAILABILITY STATEMENT

All the data supporting the results in the paper will be archived in Dryad [Itescu, Yuval; Fofopoulos, Johannes; Pafilis, Panayiotis;

Meiri, Shai (2019), The diverse nature of island isolation and its effect on land bridge insular faunas, Dryad, Dataset, <https://doi.org/10.5061/dryad.15dv41ns9>] and are available in the Supporting Information (Appendix S2).

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REFERENCES

- Adler, G. H., & Levins, R. (1994). The island syndrome in rodent populations. *The Quarterly Review of Biology*, *69*, 473–490. <https://doi.org/10.1086/418744>
- Adler, G. H., Wilson, M. L., & Derosa, M. J. (1986). Influence of island area and isolation on population characteristics of *Peromyscus leucopus*. *Journal of Mammalogy*, *67*, 406–409. <https://doi.org/10.2307/1380899>
- Ali, J. R., & Meiri, S. (2019). Biodiversity growth on the volcanic ocean islands and the roles of in situ cladogenesis and immigration: Case with the reptiles. *Ecography*, *42*, 989–999. <https://doi.org/10.1111/ecog.04024>
- Anastasakis, G., & Dermitzakis, M. (1990). Post-Middle-Miocene paleogeographic evolution of the Central Aegean Sea and detailed Quaternary reconstruction of the region. Its possible influence on the distribution of the Quaternary mammals of the Cyclades Islands. *Neues Jahrbuch für Geologie und Paläontologie*, *1*, 1–16.
- Anastasiou, I., Papadopoulou, A., & Trichas, A. (2018). Tenebrionid beetles of the Aegean archipelago: Historical review, current knowledge and future directions. In S. Sfenthourakis, P. Pafilis, A. Parmakelis, N. Poulakakis, & K. Triantis (Eds.), *Biogeography and Biodiversity of the Aegean* (honor of Prof. Moysis Mylonas, pp. 151–166). Nicosia, Cyprus: Broken Hill Publishers Ltd.
- Ås, S. (1984). To fly or not to fly? Colonization of Baltic islands by winged and wingless carabid beetles. *Journal of Biogeography*, *11*, 413–426. <https://doi.org/10.2307/2844805>
- Aubret, F. (2015). Island colonisation and the evolutionary rates of body size in insular neonate snakes. *Heredity*, *115*, 349–356. <https://doi.org/10.1038/hdy.2014.65>
- Benjamin, D. J., Berger, J. O., Johannesson, M., Nosek, B. A., Wagenmakers, E.-J., Berk, R., ... Johnson, V. E. (2018). Redefine statistical significance. *Nature Human Behaviour*, *2*, 6–10. <https://doi.org/10.1038/s41562-017-0189-z>
- Boback, S. M. (2003). Body size evolution in snakes: Evidence from island populations. *Copeia*, *2003*, 81–94. [https://doi.org/10.1643/0045-8511\(2003\)003\[0081:BSEISE\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0081:BSEISE]2.0.CO;2)
- Borges, P. A., & Brown, V. K. (1999). Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society*, *66*, 373–410. <https://doi.org/10.1111/j.1095-8312.1999.tb01897.x>
- Borges, P. A., & Hortal, J. (2009). Time, area and isolation: Factors driving the diversification of Azorean arthropods. *Journal of Biogeography*, *36*, 178–191. <https://doi.org/10.1111/j.1365-2699.2008.01980.x>
- Boyer, A. G., & Jetz, W. (2010). Biogeography of body size in Pacific island birds. *Ecography*, *33*, 369–379. <https://doi.org/10.1111/j.1600-0587.2010.06315.x>
- Brock, K. M., Bednekoff, P. A., Pafilis, P., & Fofopoulos, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? *Evolution*, *69*, 216–231.
- Brown, J. H. (1971). Mammals on mountaintops: Nonequilibrium insular biogeography. *The American Naturalist*, *105*, 467–478. <https://doi.org/10.1086/282738>

- Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, 58, 445–449. <https://doi.org/10.2307/1935620>
- Buckley, L. B., & Roughgarden, J. (2005). Effect of species interactions on landscape abundance patterns. *Journal of Animal Ecology*, 74, 1182–1194. <https://doi.org/10.1111/j.1365-2656.2005.01012.x>
- Buckley, L. B., & Roughgarden, J. (2006). Climate, competition, and the coexistence of island lizards. *Functional Ecology*, 20, 315–322. <https://doi.org/10.1111/j.1365-2435.2006.01095.x>
- Burbidge, A., Williams, M., & Abbott, I. (1997). Mammals of Australian islands: Factors influencing species richness. *Journal of Biogeography*, 24, 703–715. <https://doi.org/10.1046/j.1365-2699.1997.00145.x>
- Burkey, T. V. (1995). Extinction rates in archipelagoes: Implications for populations in fragmented habitats. *Conservation Biology*, 9, 527–541. <https://doi.org/10.1046/j.1523-1739.1995.09030527.x>
- Cabral, J. S., Whittaker, R. J., Wiegand, K., & Kreft, H. (2019). Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco-evolutionary model for plants. *Journal of Biogeography*, 46, 1569–1581. <https://doi.org/10.1111/jbi.13603>
- Cameron, R. A. D., Triantis, K. A., Parent, C. E., Guilhaumon, F., Alonso, M. R., Ibáñez, M., ... Whittaker, R. J. (2013). Snails on oceanic islands: Testing the general dynamic model of oceanic island biogeography using linear mixed effect models. *Journal of Biogeography*, 40, 117–130. <https://doi.org/10.1111/j.1365-2699.2012.02781.x>
- Case, T. J. (1975). Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology*, 56, 3–18. <https://doi.org/10.2307/1935296>
- Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, 137, 27–49. <https://doi.org/10.1086/285144>
- Dennis, R. L., & Shreeve, T. G. (1997). Diversity of butterflies on British islands: Ecological influences underlying the roles of area, isolation and the size of the faunal source. *Biological Journal of the Linnean Society*, 60, 257–275. <https://doi.org/10.1111/j.1095-8312.1997.tb01495.x>
- Dennis, R. L., Shreeve, T. G., Olivier, A., & Coutsis, J. G. (2000). Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera: Papilionoidea, Hesperioidea). *Journal of Biogeography*, 27, 1365–1383. <https://doi.org/10.1046/j.1365-2699.2000.00514.x>
- Dermitzakis, D. M. (1990). Paleogeography, geodynamic processes and event stratigraphy during the Late Cenozoic of the Aegean area. *Atti Convegno Lincei*, 85, 263–288.
- Diamond, J. M. (1972). Biogeographic kinetics: Estimation of relaxation times for avifaunas of southwest Pacific islands. *Proceedings of the National Academy of Sciences USA*, 69, 3199–3203. <https://doi.org/10.1073/pnas.69.11.3199>
- Diver, K. C. (2008). Not as the crow flies: Assessing effective isolation for island biogeographical analysis. *Journal of Biogeography*, 35, 1040–1048.
- Donihue, C. M., Brock, K. M., Fofopoulos, J., & Herrel, A. (2016). Feed or fight: Testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Functional Ecology*, 30, 566–575. <https://doi.org/10.1111/1365-2435.12550>
- Donihue, C. M., Herrel, A., Fabre, A.-C., Kamath, A., Geneva, A. J., Schoener, T. W., ... Losos, J. B. (2018). Hurricane-induced selection on the morphology of an island lizard. *Nature*, 560, 88–91. <https://doi.org/10.1038/s41586-018-0352-3>
- Fattorini, S. (2002). Biogeography of the tenebrionid beetles (Coleoptera, Tenebrionidae) on the Aegean Islands (Greece). *Journal of Biogeography*, 29, 49–67. <https://doi.org/10.1046/j.1365-2699.2002.00656.x>
- Foufopoulos, J., & Ives, A. R. (1999). Reptile extinctions on land-bridge islands: Life-history attributes and vulnerability to extinction. *The American Naturalist*, 153, 1–25. <https://doi.org/10.1086/303149>
- Foufopoulos, J., Kilpatrick, A. M., & Ives, A. R. (2011). Climate change and elevated extinction rates of reptiles from Mediterranean islands. *The American Naturalist*, 177, 119–129. <https://doi.org/10.1086/657624>
- Foufopoulos, J., & Mayer, G. C. (2007). Turnover of passerine birds on islands in the Aegean Sea (Greece). *Journal of Biogeography*, 34, 1113–1123. <https://doi.org/10.1111/j.1365-2699.2007.01695.x>
- Gibson, L., Lynam, A. J., Bradshaw, C. J. A., He, F., Bickford, D. P., Woodruff, D. S., ... Laurance, W. F. (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, 341, 1508–1510. <https://doi.org/10.1126/science.1240495>
- Grant, P. R., Grant, B. R., Huey, R. B., Johnson, M. T., Knoll, A. H., & Schmitt, J. (2017). Evolution caused by extreme events. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160146. <https://doi.org/10.1098/rstb.2016.0146>
- Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software*, 17, 1–27.
- Hamilton, T. H., & Armstrong, N. E. (1965). Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature*, 207, 148–151. <https://doi.org/10.1038/207148a0>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., ... Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. <https://doi.org/10.1890/03-8006>
- Heaney, L. R. (1984). Mammalian species richness on islands on the Sunda Shelf, southeast Asia. *Oecologia*, 61, 11–17. <https://doi.org/10.1007/BF00379083>
- Heaney, L. R. (2000). Dynamic disequilibrium: A long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, 9, 59–74. <https://doi.org/10.1046/j.1365-2699.2000.00163.x>
- Heiberger, R. M. (2009). *HH: Statistical analysis and data display: Heiberger and Holland*. R package. Retrieved from <http://CRAN.R-project.org/package=HH>
- Hellenic Statistical Authority. (2011). *Statistical yearbook of Greece 2009 & 2010*. Athens, Greece: El Stat.
- Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546. <https://doi.org/10.1038/nature13739>
- Itescu, Y. (2017). *Evolution on islands: Testing the extent and consistency of the effects of island characteristics* (Unpublished PhD thesis). Tel Aviv University, Tel Aviv, Israel.
- Itescu, Y. (2019). Are island-like systems biologically similar to islands? A review of the evidence. *Ecography*, 42, 1298–1314. <https://doi.org/10.1111/ecog.03951>
- Itescu, Y., Jamison, S., Slavenko, A., Tamar, K., Roussos, S. A., Foufopoulos, J., ... Pafilis, P. (2017). The herpetofauna of Folegandros Island (Cyclades, Greece). *Herpetozoa*, 29, 183–190.
- Itescu, Y., Schwarz, R., Donihue, C. M., Slavenko, A., Roussos, S. A., Sagonas, K., ... Meiri, S. (2018). Inconsistent patterns of body size evolution in co-occurring island reptiles. *Global Ecology and Biogeography*, 27, 538–550. <https://doi.org/10.1111/geb.12716>
- Itescu, Y., Schwarz, R., Meiri, S., & Pafilis, P. (2017). Intra-specific competition, not predation, drives lizard tail loss on islands. *Journal of Animal Ecology*, 86, 66–74. <https://doi.org/10.1111/1365-2656.12591>
- Itescu, Y., Schwarz, R., Moses, M., Pafilis, P., & Meiri, S. (2016). Record sizes for the Turkish house gecko, *Hemidactylus turcicus*, from Aegean islands, Greece. *The Herpetological Bulletin*, 138, 24–26.
- Itescu, Y., Slavenko, A., Schwarz, R., Meiri, S., & Pafilis, P. (2016). A new island record for *Chalcides ocellatus* (Forskål, 1775) from Kythnos, Greece. *Herpetozoa*, 29, 98–100.
- Jackson, D. B., Fuller, R. J., & Campbell, S. T. (2004). Long-term population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*). *Biological Conservation*, 117, 151–166. [https://doi.org/10.1016/S0006-3207\(03\)00289-1](https://doi.org/10.1016/S0006-3207(03)00289-1)
- Johnson, V. E. (2013). Revised standards for statistical evidence. *Proceedings of the National Academy of Sciences USA*, 110, 19313–19317. <https://doi.org/10.1073/pnas.1313476110>
- Kapsimalis, V., Pavlopoulos, K., Panagiotopoulos, I., Drakopoulou, P., Vandarakis, D., Sakelariou, D., & Anagnostou, C. (2009).

- Geoarchaeological challenges in the Cyclades continental shelf (Aegean Sea). *Zeitschrift für Geomorphologie*, 53(1), 169–190. <https://doi.org/10.1127/0372-8854/2009/0053S1-0169>
- Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, 175, 316–334. <https://doi.org/10.1086/650369>
- Kotsakiozi, P., Jablonski, D., Ilgaz, Ç., Kumluca, Y., Avci, A., Meiri, S., ... Poulakakis, N. (2018). Multilocus phylogeny and coalescent species delimitation in Kotschy's gecko, *Mediodactylus kotschy*: Hidden diversity and cryptic species. *Molecular Phylogenetics and Evolution*, 125, 177–187. <https://doi.org/10.1016/j.ympev.2018.03.022>
- Laliberté, E. (2011). *Metacor: Meta-analysis of correlation coefficients*. R package. Retrieved from <http://CRAN.R-project.org/package=metacor>
- Laliberté, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., ... Mayfield, M. M. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, 13, 76–86. <https://doi.org/10.1111/j.1461-0248.2009.01403.x>
- Lambeck, K. (1995). Late Pleistocene and Holocene sea-level change in Greece and south-western Turkey: A separation of eustatic, isostatic and tectonic contributions. *Geophysical Journal International*, 122, 1022–1044. <https://doi.org/10.1111/j.1365-246X.1995.tb06853.x>
- Lambeck, K. (1996). Sea-level change and shore-line evolution in Aegean Greece since Upper Palaeolithic time. *Antiquity*, 70, 588–611. <https://doi.org/10.1017/S0003598X00083733>
- Lattimore, R. (1951). *The Iliad of Homer: Translated and with an Introduction by Richard Lattimore*. Chicago, IL: University of Chicago Press.
- Lister, A. M. (1989). Rapid dwarfing of red deer on Jersey in the last interglacial. *Nature*, 342, 539–542. <https://doi.org/10.1038/342539a0>
- Littleford-Colquhoun, B. L., Clemente, C., Whiting, M. J., Ortiz-Barrientos, D., & Frère, C. H. (2017). Archipelagos of the Anthropocene: Rapid and extensive differentiation of native terrestrial vertebrates in a single metropolis. *Molecular Ecology*, 26, 2466–2481. <https://doi.org/10.1111/mec.14042>
- Lomolino, M. V. (2005). Body size evolution in insular vertebrates: Generality of the island rule. *Journal of Biogeography*, 32, 1683–1699. <https://doi.org/10.1111/j.1365-2699.2005.01314.x>
- Lomolino, M. V., Riddle, B. R., Whittaker, R. J., & Brown, J. H. (2016). *Biogeography* (5th ed.). Sunderland, MA: Sinauer Associates Inc.
- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457, 830–836. <https://doi.org/10.1038/nature07893>
- Lymberakis, P., & Poulakakis, N. (2010). Three continents claiming an archipelago: The evolution of Aegean's herpetofaunal diversity. *Diversity*, 2, 233–255. <https://doi.org/10.3390/d2020233>
- MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, 53, 330–342. <https://doi.org/10.2307/1934090>
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387. <https://doi.org/10.1111/j.1558-5646.1963.tb03295.x>
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- MacNally, R., Duncan, R. P., Thomson, J. R., & Yen, J. D. L. (2018). Model selection using information criteria, but is the 'best' model any good? *Journal of Applied Ecology*, 55, 1441–1444. <https://doi.org/10.1111/1365-2664.13060>
- Masseti, M. (2012). *Atlas of terrestrial mammals of the Ionian and Aegean islands*. Berlin, Germany: Walter de Gruyter.
- Matthews, T. J., Rigal, F., Triantis, K. A., & Whittaker, R. J. (2019). A global model of island species-area relationships. *Proceedings of the National Academy of Sciences USA*, 116, 12337–12342. <https://doi.org/10.1073/pnas.1818190116>
- Meik, J. M., Lawing, A. M., & Pires-daSilva, A. (2010). Body size evolution in insular speckled rattlesnakes (*Viperidae: Crotalus mitchellii*). *PLoS ONE*, 5, e9524. <https://doi.org/10.1371/journal.pone.0009524>
- Meiri, S. (2007). Size evolution in island lizards. *Global Ecology and Biogeography*, 16, 702–708.
- Meiri, S. (2017). Oceanic island biogeography: Nomothetic science of the anecdotal. *Frontiers in Biogeography*, 9, e32081. <https://doi.org/10.21425/F59132081>
- Meiri, S., Dayan, T., & Simberloff, D. (2005). Area, isolation and body size evolution in insular carnivores. *Ecology Letters*, 8, 1211–1217. <https://doi.org/10.1111/j.1461-0248.2005.00825.x>
- Meiri, S., Kadison, A. E., Novosolov, M., Pafilis, P., Foufopoulos, J., Itescu, Y., ... Pincheira-Donoso, D. (2014). The number of competitor species is unlinked to sexual dimorphism. *Journal of Animal Ecology*, 83, 1302–1312. <https://doi.org/10.1111/1365-2656.12248>
- Millien-Parra, V., & Jaeger, J.-J. (1999). Island biogeography of the Japanese terrestrial mammal assemblages: An example of a relict fauna. *Journal of Biogeography*, 26, 959–972. <https://doi.org/10.1046/j.1365-2699.1999.00346.x>
- Nilsson, S. G., Bengtsson, J., & Ås, S. (1988). Habitat diversity or area per se? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology*, 57, 685–704. <https://doi.org/10.2307/4933>
- Novosolov, M., Rodda, G. H., Feldman, A., Kadison, A. E., Dor, R., & Meiri, S. (2016). Power in numbers. Drivers of high population density in insular lizards. *Global Ecology and Biogeography*, 25, 87–95. <https://doi.org/10.1111/geb.12390>
- O'Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity*, 41, 673–690. <https://doi.org/10.1007/s11135-006-9018-6>
- Palmeirim, A. F., Vieira, M. V., & Peres, C. A. (2017). Non-random lizard extinctions in land-bridge Amazonian forest islands after 28 years of isolation. *Biological Conservation*, 214, 55–65. <https://doi.org/10.1016/j.biocon.2017.08.002>
- Pérez-Mellado, V., Martín-Vallejo, J., Brown, R., Picornell, A., Castro, J., Ramón, M. M., ... Hernández-Estévez, J. Á. (2008). Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphibia-Reptilia*, 29, 49–60. <https://doi.org/10.1163/156853808783431587>
- Pergams, O. R., & Ashley, M. V. (2001). Microevolution in island rodents. *Genetica*, 112, 245–256.
- Perissoratis, C., & Conispoliatis, N. (2003). The impacts of sea-level changes during latest Pleistocene and Holocene times on the morphology of the Ionian and Aegean seas (SE Alpine Europe). *Marine Geology*, 196, 145–156. [https://doi.org/10.1016/S0025-3227\(03\)00047-1](https://doi.org/10.1016/S0025-3227(03)00047-1)
- Portillo, J. T. D. M., Ouchi-Melo, L. S., Crivellari, L. B., Oliveira, T. A. L., Sawaya, R. J., & Duarte, L. D. S. (2019). Area and distance from mainland affect in different ways richness and phylogenetic diversity of snakes in Atlantic Forest coastal islands. *Ecology and Evolution*, 9, 3909–3917. <https://doi.org/10.1002/ece3.5019>
- Poulakakis, N., Kapli, P., Lymberakis, P., Trichas, A., Vardinoyiannis, K., Sfenthourakis, S., & Mylonas, M. (2014). A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research*, 53, 18–32.
- Poulos, S. E., Ghionis, G., & Maroukian, H. (2009). Sea-level rise trends in the Attico-Cycladic region (Aegean Sea) during the last 5000 years. *Geomorphology*, 107, 10–17.
- Rosindell, J., & Phillimore, A. B. (2011). A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, 14, 552–560. <https://doi.org/10.1111/j.1461-0248.2011.01617.x>
- Ryan, W. B. F., Carbotte, S. M., Coplan, J. O., O'Hara, S., Melkonian, A., Arko, R., ... Zemsky, R. (2009). Global multi-resolution topography synthesis. *Geochemistry, Geophysics, Geosystems*, 10, Q03014. <https://doi.org/10.1029/2008GC002332>
- Sakellariou, D., & Galanidou, N. (2016). Pleistocene submerged landscapes and Palaeolithic archaeology in the tectonically active Aegean region. *Geological Society, London, Special Publications*, 411, 145–178. <https://doi.org/10.1144/SP411.9>

- Santos, A., Field, R., & Ricklefs, R. E. (2016). New directions in island biogeography. *Global Ecology and Biogeography*, 25, 751–768.
- Sfenthourakis, S. (1996). The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): A comparative study. *Global Ecology and Biogeography Letters*, 5, 149–157. <https://doi.org/10.2307/2997397>
- Sfenthourakis, S., Pafilis, P., Parmakelis, A., Poulakakis, N., & Triantis, K. A. (2018). *Biogeography and biodiversity of the Aegean* (honor of Prof. Moysis Mylonas). Nicosia, Cyprus: Broken Hill Publishers Ltd.
- Sfenthourakis, S., & Triantis, K. A. (2009). Habitat diversity, ecological requirements of species and the small island effect. *Diversity and Distributions*, 15, 131–140. <https://doi.org/10.1111/j.1472-4642.2008.00526.x>
- Sfenthourakis, S., & Triantis, K. A. (2017). The Aegean archipelago: A natural laboratory of evolution, ecology and civilisations. *Journal of Biological Research-Thessaloniki*, 24, 4. <https://doi.org/10.1186/s40709-017-0061-3>
- Simaiakis, S. M., Dretakis, M., Barboutis, C., Katritis, T., Portolou, D., & Xirouchakis, S. (2012). Breeding land birds across the Greek islands: A biogeographic study with emphasis on faunal similarity, species-area relationships and nestedness. *Journal of Ornithology*, 153, 849–860. <https://doi.org/10.1007/s10336-011-0803-1>
- Simaiakis, S., Minelli, A., & Mylonas, M. (2005). The centipede fauna (Chilopoda) of the south Aegean archipelago (Greece, eastern Mediterranean). *Israel Journal of Zoology*, 51, 241–307.
- Simaiakis, S. M., Rijdsdijk, K. F., Koene, E. F. M., Norder, S. J., Van Boxel, J. H., Stocchi, P., ... Tjørve, E. (2017). Geographic changes in the Aegean Sea since the Last Glacial Maximum: Postulating biogeographic effects of sea-level rise on islands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 471, 108–119. <https://doi.org/10.1016/j.palaeo.2017.02.002>
- Stuart, Y. E., Campbell, T., Hohenlohe, P., Reynolds, R. G., Revell, L., & Losos, J. (2014). Rapid evolution of a native species following invasion by a congener. *Science*, 346, 463–466. <https://doi.org/10.1126/science.1257008>
- Triantis, K. A., Vardinoyannis, K., & Mylonas, M. (2008). Biogeography, land snails and incomplete data sets: The case of three island groups in the Aegean Sea. *Journal of Natural History*, 42, 467–490. <https://doi.org/10.1080/00222930701835431>
- Trichas, A., Lagkis, A., Triantis, K. A., Poulakakis, N., & Chatzaki, M. (2008). Biogeographic patterns of tenebrionid beetles (Coleoptera, Tenebrionidae) on four island groups in the south Aegean Sea. *Journal of Natural History*, 42, 491–511. <https://doi.org/10.1080/00222930701835472>
- Van Andel, T. H., & Shackleton, J. C. (1982). Late Paleolithic and Mesolithic coastlines of Greece and the Aegean. *Journal of Field Archaeology*, 9, 445–454.
- Vujić, A., Petanidou, T., Tscheulin, T., Cardoso, P., Radenković, S., Ståhls, G., ... Pérez-Bañón, C. (2016). Biogeographical patterns of the genus *Merodon* Meigen, 1803 (Diptera: Syrphidae) in islands of the eastern Mediterranean and adjacent mainland. *Insect Conservation and Diversity*, 9, 181–191.
- Wang, S., Zhu, W., Gao, X. U., Li, X., Yan, S., Liu, X., ... Li, Y. (2014). Population size and time since island isolation determine genetic diversity loss in insular frog populations. *Molecular Ecology*, 23, 637–648. <https://doi.org/10.1111/mec.12634>
- Watling, J. I., & Donnelly, M. A. (2006). Fragments as islands: A synthesis of faunal responses to habitat patchiness. *Conservation Biology*, 20, 1016–1025.
- Weigelt, P., & Kreft, H. (2013). Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography*, 36, 417–429. <https://doi.org/10.1111/j.1600-0587.2012.07669.x>
- Weigelt, P., Steinbauer, M. J., Cabral, J. S., & Kreft, H. (2016). Late Quaternary climate change shapes island biodiversity. *Nature*, 532, 99–102. <https://doi.org/10.1038/nature17443>
- Welter-Schultes, F., & Williams, M. (1999). History, island area and habitat availability determine land snail species richness of Aegean islands. *Journal of Biogeography*, 26, 239–249. <https://doi.org/10.1046/j.1365-2699.1999.00276.x>
- Whittaker, R. J., & Fernández-Palacios, J. M. (2006). *Island biogeography: Ecology, evolution, and conservation* (2nd ed.). Oxford, UK: Oxford University Press.
- Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: Taking the long view of nature's laboratories. *Science*, 357, eaam8326. <https://doi.org/10.1126/science.aam8326>
- Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, 35, 977–994.
- Wilcox, B. A. (1978). Supersaturated island faunas: A species-age relationship for lizards on post-Pleistocene land-bridge islands. *Science*, 199, 996–998. <https://doi.org/10.1126/science.199.4332.996>
- Willemsse, L., Kleukers, R., & Odé, B. (2018). *The grasshoppers of Greece*. Leiden, The Netherlands: European Invertebrate Survey.

BIOSKETCH

Yuval Itescu is interested in biogeographical patterns, the processes shaping biodiversity at all spatial scales, and the way in which natural and anthropogenic factors affect the evolution and ecology of animal traits. He is especially fascinated by the implications of urban and insular environments on the ecology and evolution of their fauna.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1. DATA SOURCES

- Beerli, P., Hotz, H., & Uzzell, T. (1996). Geologically dated sea barriers calibrate a protein clock for Aegean water frogs. *Evolution*, 50, 1676–1687.
- Comes, H. P., Tribsch, A., & Bittkau, C. (2008). Plant speciation in continental island floras as exemplified by *Nigella* in the Aegean Archipelago. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3083–3096.
- Dermitzakis, D. M. (1990). Paleogeography, geodynamic processes and event stratigraphy during the Late Cenozoic of the Aegean area. *Atti Convegno Linnei*, 85, 263–288.
- Fytikas, M., Innocenti, F., Kolios, N., Manetti, P., Mazzuoli, R., Poli, G., ... Villari, L. (1986). Volcanology and petrology of volcanic products from the island of Milos and neighbouring islets. *Journal of Volcanology and Geothermal Research*, 28, 297–317.

- Fytikas, M., & Vougioukalakis, G. (2005). *The south Aegean active volcanic arc: Present knowledge and future perspectives*. Amsterdam: Elsevier.
- Global Volcanism Program. (2013). *Volcanoes of the World*, v.4.5.4. In E. Venzke (Ed.). Washington DC: Smithsonian Institution. Retrieved from <http://dx.doi.org/10.5479/si.GVP.VOTW4-2013>
- Kasapidis, P., Magoulas, A., Mylonas, M., & Zouros, E. (2005). The phylogeography of the gecko *Cyrtopodion kotschy* (Reptilia: Gekkonidae) in the Aegean archipelago. *Molecular Phylogenetics and Evolution*, 35, 612–623.
- Kornilios, P., Poulakakis, N., Mylonas, M., & Vardinoyannis, K. (2009). The phylogeny and biogeography of the genus *Zonites* Montfort, 1810 (Gastropoda: Pulmonata): preliminary evidence from mitochondrial data. *Journal of Molluscan Studies*, 75, 109–117.
- Kougioumoutzis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660.
- Lambeck, K. (1996). Sea-level change and shore-line evolution in Aegean Greece since Upper Palaeolithic time. *Antiquity*, 70, 588–611.
- Nomikou, P., Papanikolaou, D., Alexandri, M., Sakellariou, D., & Rousakis, G. (2013). Submarine volcanoes along the Aegean volcanic arc. *Tectonophysics*, 597, 123–146.
- Papanikolaou, D., Lekkas, E., & Sakellariou, D. (1991) Geological structure and evolution of the Nisyros Volcano. *Bulletin of the Geological Society of Greece*, 25, 405–419.
- Parmakelis, A., Stathi, I., Spanos, L., Louis, C., & Mylonas, M. (2006). Phylogeography of *Iurus dufourei* (Brulle, 1832) (Scorpiones, Iuridae). *Journal of Biogeography*, 33, 251–260.
- Poulakakis, N., Kapli, P., Lymberakis, P., Trichas, A., Vardinoyannis, K., Sfenthourakis, S., & Mylonas, M. (2014). A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions. *Journal of Zoological Systematics and Evolutionary Research*, 53, 18–32.
- Poulakakis, N., Lymberakis, P., Valakos, E., Zouros, E., & Mylonas, M. (2005). Phylogenetic relationships and biogeography of *Podarcis* species from the Balkan Peninsula, by Bayesian and maximum likelihood analyses of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 37, 845–857.
- Spiteri, S. (2001). *Fortresses of the knights*. San Ġwann, Malta: Book Distributors Limited.
- Trichas, A., Lagkis, A., Triantis, K. A., Poulakakis, N., & Chatzaki, M. (2008). Biogeographic patterns of tenebrionid beetles (Coleoptera, Tenebrionidae) on four island groups in the south Aegean Sea. *Journal of Natural History*, 42, 491–511.